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Arctia menetriesii: Ecological, phenological, and life history traits of an iconic boreal moth based on over a century-long dataset (Lepidoptera, Erebidae, Arctiinae)

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Abstract. The Menetries' Tiger Moth *Arctia menetriesii* can be considered a prospective umbrella/indicator/flagship species for conservation programs, highlighting primeval Eurasian taiga forests. To examine its inter-annual population dynamics, host plants, habitat preferences and phenology, a dataset from field surveys and experimental research was compiled. The species' rarity may be, at least partly, an artifact of its low detectability in nature due to its preference for hard-to-reach areas, short flight period of the imago, and, perhaps,

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limited daily activity. The natural survival patterns of *A. menetriesii* are still unknown but in breeding experiments maximum mortality occurred at the larval stage (mean ± S.E. = 84.6 ± 6.2%; $n = 7$). This estimate does not take into account the potential impact of parasitoids, predators, and floods that may also decrease the total abundance of *A. menetriesii*. Moreover, several limiting factors may contribute to the extreme rarity of this species: climate influence, dependence on toxic host plants, fungal disease and desiccation in overwintering larvae. Our research indicates that there are clear differences between European and Asian populations of the species. In Europe, it occurs more rarely, in odd years, and with restricted latitudinal, elevational, and habitat ranges, perhaps due to the founder effect. Our findings reveal that long-term series of *A. menetriesii* annual captures do not align with the global trend of insect declines. Further research is necessary to create a climatic niche model and to assess possible range shifts under past and future climate scenarios.

Introduction

A plethora of recent studies have documented an alarming tendency towards global and rapid declines in insect biomass and diversity during the last decades (Goulson 2019; Van Klink et al. 2020; Chowdhury et al. 2023a; Finn et al. 2023). These declines strongly influence multiple ecosystem services and trophic interactions supported by insects (Sánchez-Bayo and Wyckhuys 2019; Wagner 2020; Uhler et al. 2021). Moreover, this negative trend may coincide with local, regional, and global extinctions of certain insect species, especially those having narrow ecological requirements and low abundance (Fonseca 2009; Cardoso et al. 2020; Thomas et al. 2004). Hence, such ecological specialists need special research on possible limiting factors to develop conservation action plans (New 2004; Samways et al. 2020; Chowdhury et al. 2023b). Covering the entire species diversity of insects by autecological surveys is next to impossible even in lower-diverse boreal and Arctic faunas but some notable examples could be selected as umbrella species, whose protection may help to conserve specific types of habitats with their animal and plant communities (the so-called umbrella effect) (Roberge and Angelstam 2004; Branton and Richardson 2011; Morán-López et al. 2020).

The Menetries' Tiger Moth *Arctia menetriesii* (Eversmann, 1846) (Lepidoptera: Erebidae) is an iconic, large and colourful insect, preferring primary boreal (taiga) forests (Bolotov et al. 2022a). This moth fulfills the criteria of umbrella, indicator, and flagship species such as popularity, large size, bright colours and strict preference to natural (undisturbed) habitats (New 1997; New 2011; Barua et al. 2012). It may also be considered one of the world's rarest tiger moth species based on the low number of specimen records (Bolotov et al. 2013a; Saarenmaa 2021; Bolotov et al. 2022a). This species was described based on a single specimen (the holotype by monotypy) that was collected in the mountains of East Kazakhstan ("Songoria") in the early 1840s (Eversmann 1846). The second specimen was discovered near Yakutsk, Eastern Siberia approximately 60 years later, while the third moth was collected from Finland in 1913 (Fabritius 1914). Earlier authors paid full attention to the enormous range disjunctions between records from Finland and Northern Asia (Filipiev 1916; Krogerus 1944; Kurentzov 1965; Dubatolov 2004). It was assumed that the species should occur in those distribution gaps but is largely overlooked there due to its preference for specific habitats and the deficiency of field sampling efforts in hard-to-reach areas (Krogerus 1944). Further occurrence reports revealed that the range of *A. menetriesii* is indeed more continuous than it was expected and that it spreads throughout taiga forests of Eurasia from Finland and European Russia through the Urals and Western Siberia to the Far East (including Northeastern China and the Sakhalin Island) (Nupponen and Fibiger 2012; Bolotov et al. 2013a; Bolotov et al. 2022a).

Previously, our team collected data on available occurrences of *A. menetriesii* from the 1840s to 2020 that were compiled into an online database on its records and ecology (Bolotov et al. 2022a; Bolotov et al. 2022b). Based on this over a century-long time series of occurrence data from Europe, Siberia, and the Far East, the present study (1) estimates general patterns of the long-term dynamics of annual captures of this moth in relation to climate fluctuations; (2) assesses its host plant preferences, habitat breadth, and phenological patterns by means of a comparative statistical approach; (3) highlights possible reasons that may contribute to the exceptional rarity (or low detectability) of *A. menetriesii* at the continental scale; and (4) discusses these results within a broader ecological context linked to insect declines in the Anthropocene.

Methods

Database of *A. menetriesii* occurrences and the limitations of the annual capture data

Reliable records of *A. menetriesii* from 1840s to 2020 (n = 78) were compiled in a database, which is deposited on Figshare (Bolotov et al. 2022a; Bolotov et al. 2022b). The database contains original data, information from published sources, and records from state and private collections (Bolotov et al. 2022a). The authors of this paper were searching for *A. menetriesii* specimens under the framework of their annual field work from the early 1990s to 2023. The specimens were sampled by an entomological net or by hand. Our field trips covered Finland (RH, HS, MT; one imago in 2011), European Russia and the Ural Mountain Range (INB, MYG, VVG, YSK, GSP, VMS, HS; one imago in 2005), Western Siberia (EGS; three imagoes in 2002), Eastern Siberia (OEB, SYG, TVG, SSS, HS, MT; two imagoes in 1999, one imago in 2012, two larvae in 2013, and one imago in 2018), and the Russian Far East (ESK, YIB; two imagoes – in 2018 and 2020) (Bolotov et al. 2022b). In total, 13 specimens of *A. menetriesii* (eight living and three dead imagoes, and two larvae) were sampled from across Northern Eurasia by 15 collectors based on annual (June-August) collecting efforts for over a 30-year period.

The database contains the following fields: locality, its geographic co-ordinates, their uncertainty, elevation, region, country; ecoregions, habitat type, presence/absence of a waterbody; collecting day, ten-day-period, month, and year of a given record; in which (odd or even) year the specimen was collected; developmental stage (larva, imago, etc.); sex (imaginal records only); and condition (living or dead individual) (Bolotov et al. 2022b). A complete description of the data collecting approaches and the resulting database is presented in a Data Descriptor article (Bolotov et al. 2022a).

We selected nearly all reliable records of this species during over a century-long period and estimated that the number of overlooked records may not be higher than 10–15% of the total number of records in our database (Bolotov et al. 2022a). However, *A. menetriesii* is an extremely rare (or hardly detectable in nature) species. The limited number of its available records (mostly presented by singletons) imposes certain restrictions on the application of statistical analyses and on our conclusions for ecological, phenological, and life history patterns.

Influence of climate (temperature) variables on long-term series of *A. menetriesii* occurrences

Annual captures of this species were designed as time series for the species' entire range (Eurasia) and for each region separately (Europe, Siberia, and the Far East) (Suppl. material 1). Accordance between the time series of annual captures in different regions was assessed with the Spearman's rank correlation coefficient (Lebl et al. 2013; Puth et al. 2015). The differences of

Spearman's coefficients from zero were assessed using Monte Carlo Randomization test with 1000 replications using R v. 4.0.1 (R Core Team 2020).

Monthly mean air temperatures for each sampling locality of *A. menetriesii* from 1901 to 2020 were obtained from CRU TS v. 4.05 (Climatic Research Unit gridded Time Series), representing a global dataset on a 0.5° latitude by 0.5° longitude grid (Harris et al. 2020). The climate dataset was processed using the Climate Data Operators (CDO) (Schulzweida 2019) and ESRI ArcGIS 10 software (https://www.esri.com/arcgis). The monthly data were averaged by region and by the entire range (Suppl. material 1). Sympatric occurrences were treated as a single locality. Localities with uncertain coordinates (one record from East Kazakhstan and three records from China) were excluded from the averaging. Annual mean air temperatures for each region and for the entire range were calculated based on the monthly mean data (Suppl. material 1). Additionally, principal component analyses (PCA) were performed on monthly mean air temperatures from each region and from the entire range using PAST v. 4.17 software (Hammer et al. 2001). The principal component 1 (PC1) time series generated with PCA were used as a supplemental climate variable (Suppl. material 1) in subsequent cross-correlation analyses (see below). We did not use other climate variables such as the temperature extremes and amounts of precipitation. They are characterized by a higher regional and local variability compared with air temperature values and are less appropriate for averaging through large regions.

We applied a cross-correlation approach using the Spearman's rank correlation coefficient (ρ) (Lebl et al. 2013; Puth et al. 2015) to find possible deferred effects of climatic fluctuations on *A. menetriesii*. These analyses were performed with STATISTICA v. 13.3. As climate variables, we used monthly and annual mean air temperatures, and PC1 of monthly mean air temperatures. As an indirect indicator of population dynamics, we used data on annual captures of this species by region and by the entire range with a time lag of 0 to 10 years. A series of cross-correlation maps were created using a dataset of Spearman's coefficients generated in these runs (Suppl. material 2).

Environmental preferences and phenological analyses

To estimate latitude as a possible predictor for the altitude of collecting localities, we used a simple exponential regression model (Sokal and Rohlf 2009) of STATISTICA v. 13.3 (Stat Soft Inc., USA), because this model showed the best approximation compared with the linear regression model. Three Siberian (occurrence IDs: AM-044; AM-047; and AM-048) and one Far Eastern (occurrence ID: AM-069) occurrences revealed outlier (anomalous) altitudinal observations in relation to latitude. These variables were excluded from the regression analyses based on available recommendations (Sokal and Rohlf 2009).

The observation data on environmental preferences and phenological patterns were processed in Microsoft Excel and R v. 4.0.1 using basic functions (R Core Team 2020). The Pearson's chi-squared test (χ^2) was used to assess the accordance of observed data to the discrete uniform distribution, and to estimate the significance of empiric differences between frequencies. The variability ranges for each median value were estimated using a simple non-parametric bootstrapping approach ($B = 1000$ replications) (Shitikov and Rozenberg 2013). The confidence interval boundaries of variation series were established by means of a percentile method. The Monte Carlo Randomization test with 1000 replications was applied to assess the differences of median values from zero. The level of significance p represents the adjusted share of null-model combinations (the empirical difference of values is not greater than the randomised difference, $|d_{obs}| \leq |d_{ran}|$) in the total number of tests B. The standard significance level $\alpha = 0.05$ was taken as the critical p-value.

To assess possible climate-based differences between groups of localities of *A. menetriesii* by region and between areas with odd- and every-year appearance of imago, we applied linear discriminant analysis (LDA) based on monthly mean air temperature characteristics using PAST v. 4.17 (Hammer et al. 2001).

Breeding experiments, host plant preferences, and the limitations of experimental data

Here, we compiled data from five breeding experiments on *A. menetriesii*. The experiments aimed to (1) examine the life history of the species, including the survival, mortality and metamorphosis patterns under different feeding and hibernation regimes; and (2) determine its host-plant spectrum. The conditions and brief summary of each experiment are presented in Suppl. material 7: table S1. Each experiment was based on eggs that were obtained from one wild-caught, mated female (total $n = 5$; occurrence IDs AM-002, AM-037, AM-035, AM-042, AM-066) (Krogerus 1944; Koshkin 2021; Saarenmaa 2021; Bolotov et al. 2022a; Bolotov et al. 2022b).

The first experiment was performed by Krogerus (1944) in 1943–1944 using the female AM-002 from Finland. Altogether 30 larvae were bred on a mixed diet using *Taraxacum* sp. with supplement of a few other herbs (unspecified Asteraceae, *Plantago* sp., and *Polygonum* [*Persicaria*?] sp.) with hibernation under natural (outdoor) conditions but only two of them developed into adults.

The second experiment was performed in 2011–2012 based on eggs that were obtained from the female AM-037 from Eastern Siberia. It was designed in two independent replications: (1) 23 larvae were bred on a mixed diet (*Taraxacum* sp., *Plantago* sp., *Larix* sp. and others) in Eastern Siberia with hibernation under natural (outdoor) conditions, and six of them developed into imagoes (researchers: O.V. Korsun & N.O. Korsun); and (2) 80 larvae were bred on a similar diet in Finland with hibernation under both natural and laboratory conditions, and seven of them developed into imagoes (researchers: H. Saarenmaa et al.).

The third experiment was performed in 2012–2013 based on eggs that were obtained from the female AM-035 from Eastern Siberia. Altogether 120 larvae were bred on a mixed diet (Grossulariaceae: *Ribes nigrum* L., and Rosaceae: *Fragaria* × *ananassa* Duchesne, *Malus baccata* (L.) Borkh., *Prunus domestica* L., and *Rubus idaeus* L.) with hibernation under natural (outdoor) conditions in Eastern Siberia. Most of the larvae ($n = 110$) died before hibernation due to unclear reasons, while the rest of larvae died during hibernation (researchers: S.Y. Gordeev and T.V. Gordeeva).

The fourth experiment was performed in 2018–2019 based on eggs that were obtained from the female AM-042 from Eastern Siberia. It was designed in two independent replications: (1) 40 larvae were bred on *Rubus idaeus* in Eastern Siberia but all of them died during hibernation under natural (outdoor) conditions due to the extremely low winter temperatures (researchers: S.Y. Gordeev & T.V. Gordeeva); and (2) 90 larvae were bred on a mixed diet with addition of *Larix* spp. in Finland with and without hibernation (81 and nine larvae, respectively), and 33 of them developed into imagoes, including two adults with developmental anomalies (researchers: M. Tähtinen et al.). Additional information on M. Tähtinen et al.'s breeding experiment of 2018–2019 in Finland is given in Suppl. material 7: note S1.

Finally, the fifth experiment was based on eggs obtained from the female AM-066 from the Far East. It was performed and described by Koshkin (2021). Altogether 105 larvae were bred on a mixed diet in two groups (with and without addition of the strongly toxic plant *Aconitum consanguineum* Borosch. (Ranunculaceae), see below) without hibernation; 14 of them were developed into imagoes, including those with multiple developmental anomalies (Suppl. material 7: table S1 and Suppl. material 5).

Data from three breeding experiments (female mouther IDs: AM-002, AM-037, and AM-066; see Suppl. material 7: table S1 for detail) were compiled to survival tables (Suppl. materials 5, 6) and processed with Kaplan-Meier estimator (Sokal and Rohlf 2009) using STATISTICA v. 13.3.

It was shown that larvae of *A. menetriesii* are polyphagous and could feed on a variety of host plants, some of which are strongly toxic (*Aconitum* spp.) (Bolotov et al. 2013a; Berlov and Bolotov 2015; Koshkin 2021; Saarenmaa 2021). Information on host plant preferences of the larvae is based on field observations and experimental data. In total, ten observers tested 52 plant and one lichen species to find suitable host plants of *A. menetriesii* (Suppl. material 4). The majority of the tested plant species were chosen because they occur in the sampling localities of *A. menetriesii*. Field data on native host plants is limited to a single paper that documents feeding of wild larvae on the strongly toxic plant *Aconitum rubicundum* (Ser.) Fisch. ex C.Young, J.Young & P.Young in Eastern Siberia (Berlov and Bolotov 2015). Koshkin (2021) examined feeding, survival, and metamorphosis of larvae under laboratory conditions using *A. consanguineum* as treatment and non-toxic plants as control (Suppl. materials 4, 5). Saarenmaa (2021) curated a series of experiments performed by amateur researchers, who offered various plants to different groups of larvae. S. Y. Gordeev and T. V. Gordeeva discovered several additional host plants during their breeding experiment (Suppl. material 4 and Suppl. material 7: table S1). Observers checked whether a given plant is used for consumption or not (accepted host plant vs. non-consumed plant – see Suppl. material 4 for detail). The toxicity of host plants was evaluated using the TPPT (Toxic Plants–PhytoToxins) Database (Günthardt et al. 2018) with supplement of a few other sources (Manoliu 1975; Titovich et al. 2009; Kubinova et al. 2014; Jansone et al. 2017; Sepahvand et al. 2021; The PLANTS Database 2021).

It should be noted that the data on host plants, survival and mortality of this species are largely based on a series of laboratory experiments (see below) that may create a bias towards our conclusions. For instance, egg mortality in the five experiments was very low due to the elimination of egg parasitoid impact, because the eggs were produced by captive females in laboratory conditions. Eggs of only five wild females were used in experiments and the possible influence of maternal effects (e.g. Mousseau and Dingle 1991) on our results cannot be ruled out.

Data availability statement

This study is based on the Menetries' Tiger Moth Range and Ecology Database (1840s–2020), which was described in a separate Data Descriptor article (Bolotov et al. 2022a). The database can be downloaded from Figshare (Bolotov et al. 2022b; https://doi.org/10.6084/m9.figshare.15000399). The climate variables used in this study are presented in Suppl. material 1. The results of cross-correlation, autocorrelation, and spectral analyses are presented in Suppl. materials 2, 3. Host plant preferences of the larvae based on several experimental surveys and field observations are given in Suppl. material 4. Available survival data from breeding experiments is given in Suppl. materials 5, 6. Additional data from breeding experiments and fieldwork used in this study is presented in Suppl. material 7.

Results

Total number of *A. menetriesii* occurrences by region

Data on 78 occurrences of this extremely rare species were compiled in our online database (Bolotov et al. 2022a; Bolotov et al. 2022b). Most annual samples from each region are represented by singletons but, in a few cases, 2–5 specimens were collected from one region per year (Suppl.

material 7: fig. S1). The largest number of specimens was collected from Siberia (Russia and East Kazakhstan; $n = 43$), followed by the Far East (Russia and China; $n = 24$) and Europe (Finland and Russia; $n = 11$) (Fig. 1a–d). Altogether 69 captures in the database are linked to a certain year. The cumulative number of annual captures shows rather different long-term patterns in each region (Fig. 2a). In Europe, there was a gap between 1943 and 2003, with a few subsequent records from 2003 to 2011. In Siberia, the number of captures slowly increased from 1900s to 1980s, followed by an exponential growth until the late 2010s. In the Far East, there were a few captures and some

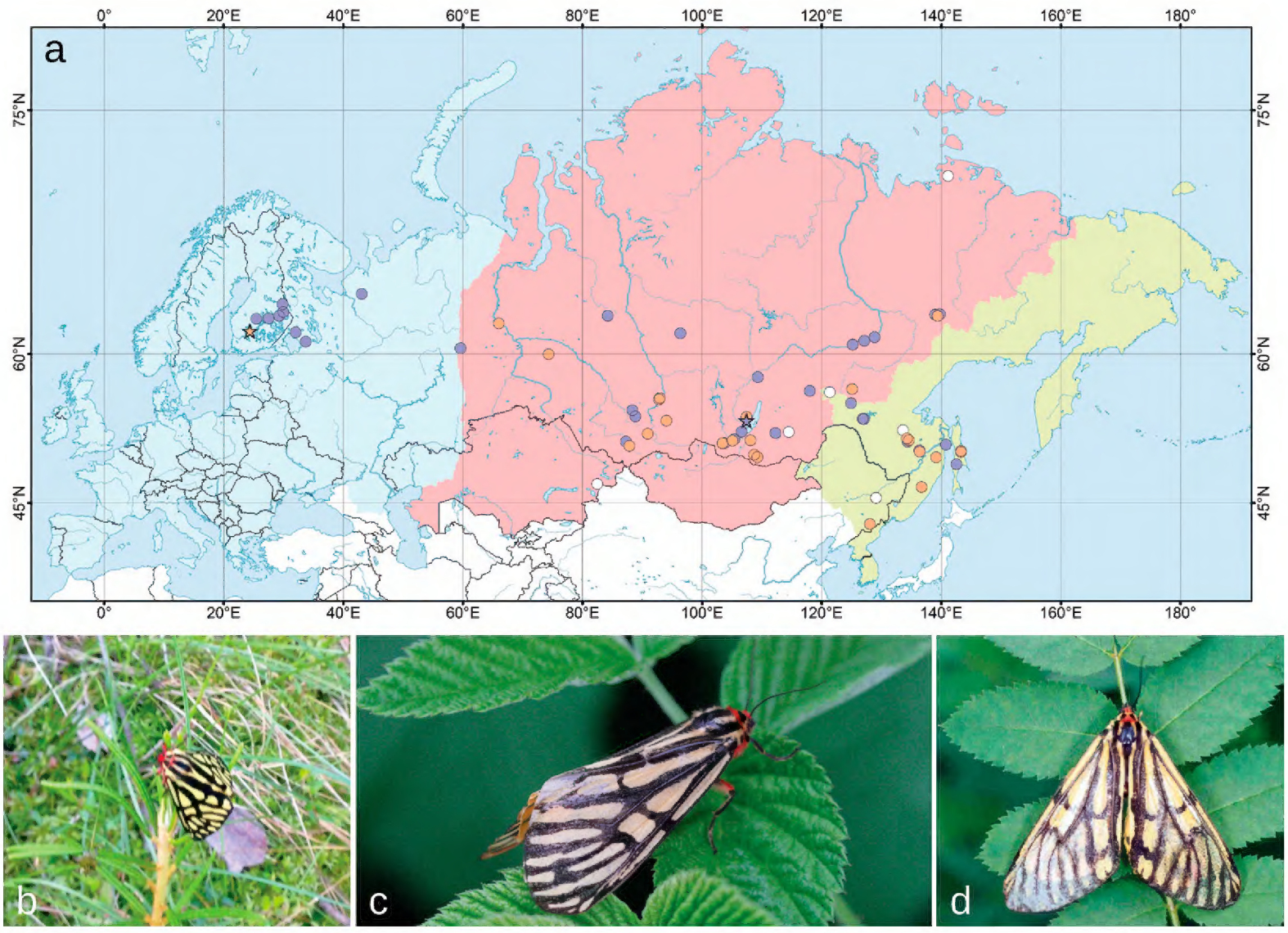

Figure 1. Range, periodical appearance, and imago of *Arctia menetriesii*. **a.** Map of distribution showing occurrences in odd and even years. The circles show imaginal captures as follows: dark blue odd years; light orange even years; and white unknown years. The stars show larval captures (colours as for the imagoes). The coloured areas represent three larger regions as follows: light blue Europe (records from Finland, Northern European Russia, and the Urals); light red Siberia (records from Western and Eastern Siberia in Russia, and eastern Kazakhstan); and light green the Far East (records from the Russian Far East and northeastern China). The map was created using ESRI ArcGIS 10 software (https://www.esri.com/arcgis); the topographic base of the map was compiled with Natural Earth Free Vector and Raster Map Data (https://www.naturalearthdata.com) and Global Self-consistent Hierarchical High-resolution Geography, GSHHG v2.3.7 (https://www.soest.hawaii.edu/wessel/gshhg). Map: Mikhail Y. Gofarov. **b.** Freshly emerged male from Kuhmo, Vattuvaara, Finland, 25 June 2011 (occurrence ID: AM-007). **c.** Living female from Onokhoy settlement, Uda River valley, Republic of Buryatia, Eastern Siberia, Russia, 11 July 2012 (occurrence ID: AM-035). **d.** Dead female collected in debris at a river site blocked by fallen tree trunks and branches, Negusyakh River valley, Yugansky State Nature Reserve, Khanty-Mansi Region, Western Siberia, Russia, 02 July 2002, occurrence ID: AM-016. Photos: Risto Haverinen (**b**); Sergey Y. Gordeev (**c**); and Evgeny G. Strelnikov (**d**).

long-term gaps until 1975, followed by a gradual growth up to 2020. However, the cumulative number of annual captures in all the regions rapidly increased since the 1990–2000s.

The median altitude of *A. menetriesii* localities in Europe is significantly lower compared with those in Siberia and the Far East (Monte Carlo Randomization test; $p \leq 0.024$), while the medians for the two latter regions do not differ from each other (Monte Carlo Randomization test; $p = 0.442$) (Fig. 2c). The altitude of localities plotted against latitude shows a significant exponential trend (Fig. 2d). Three highland localities from the Suntar-Khayata Mountain Ridge in Eastern Siberia (occurrence IDs: AM-044, AM-047, and AM-048; Bolotov et al. 2022a; Bolotov et al. 2022b) and one plain locality from the Okhotsk Sea coast in the Far East (occurrence ID: AM-069; Bolotov et al. 2022a; Bolotov et al. 2022b) were excluded as outlier observations based on initial statistical assessment, because these records may belong to vagrant individuals or deviant (e.g. high-elevation) populations (see Discussion).

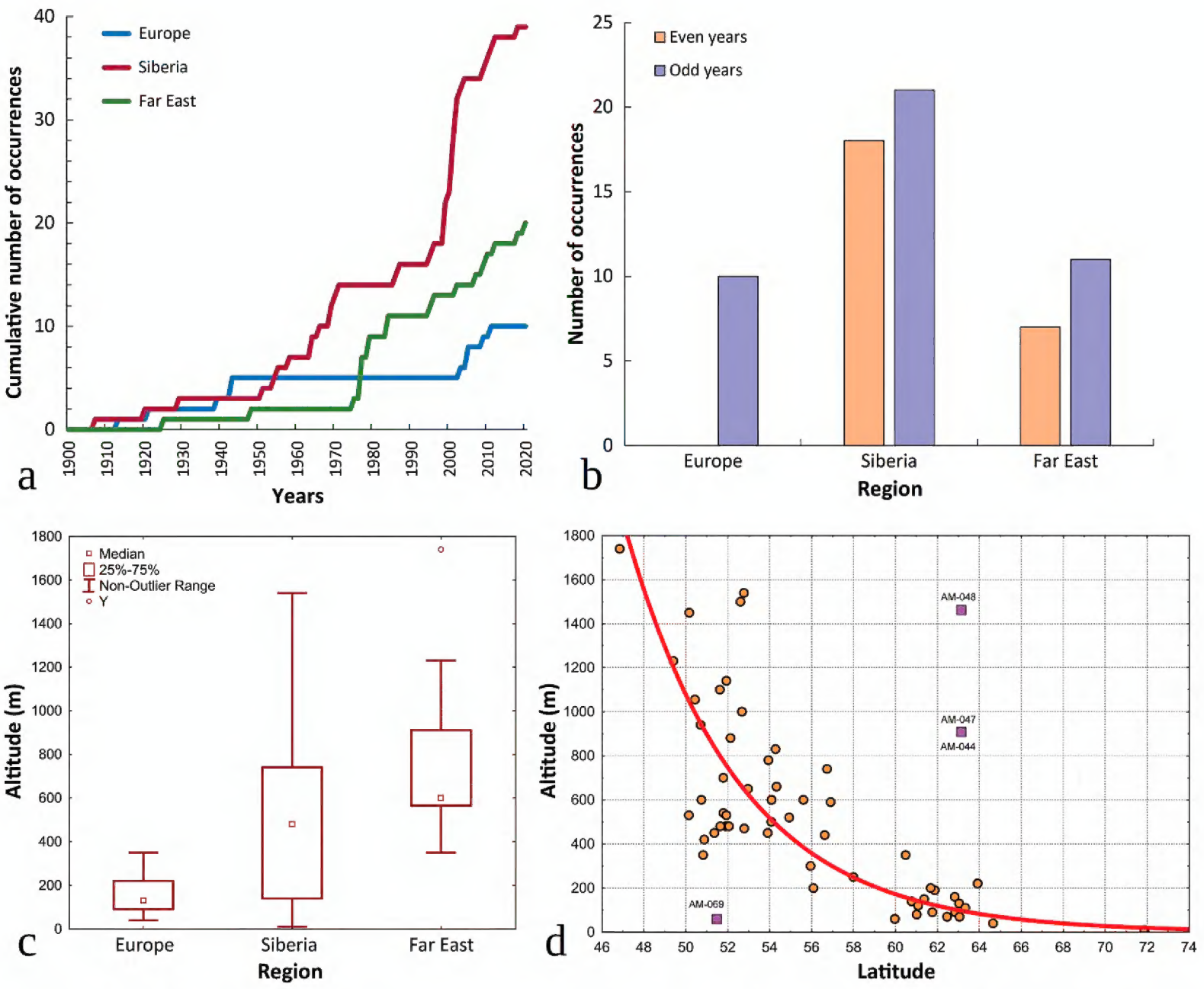

Figure 2. Total number of *Arctia menetriesii* captures by region and geographic characteristics of its localities. **a.** Cumulative number of annual captures by region. **b.** Total number of imaginal captures in each region through even and odd years. **c.** Boxplot showing the median altitude of collecting localities by region, with percentiles and non-outlier range. **d.** Latitude vs. altitude scatterplot of the collecting localities across the entire species range (Eurasia). The solid line shows an exponential trend: Altitude (km) = 10,370.45 × *exp* (-0.18 × Latitude); $n = 68$; $R^2 = 0.77$; $p < 0.001$. Four anomalous observations (purple squares: three Siberian and one Far Eastern localities; see Methods section) were excluded from the trend calculation.

Patterns of the long-term dynamics of *A. menetriesii* inter-annual captures

Time series of *A. menetriesii* annual captures from the three regions significantly differ from the discrete uniform distribution (Pearson's chi-squared test: $\chi^2 > 159.4$; $df = 120$; $p < 0.002$), with the largest difference for Siberian and the smallest difference for European series (Fig. 3a–c). The highest density of annual captures throughout Eurasia corresponds to the period of 1990–2000s (Fig. 3d). The time series from Siberia and the Far East are significantly linked to each other but with a rather low similarity (Spearman's $\rho = 0.205$, $n = 121$, $p = 0.024$), while its dynamics in Europe does not fit those in both Asian regions (Spearman's $\rho < 0.083$, $n = 121$, $p > 0.366$) (Suppl. material 7: fig. S2).

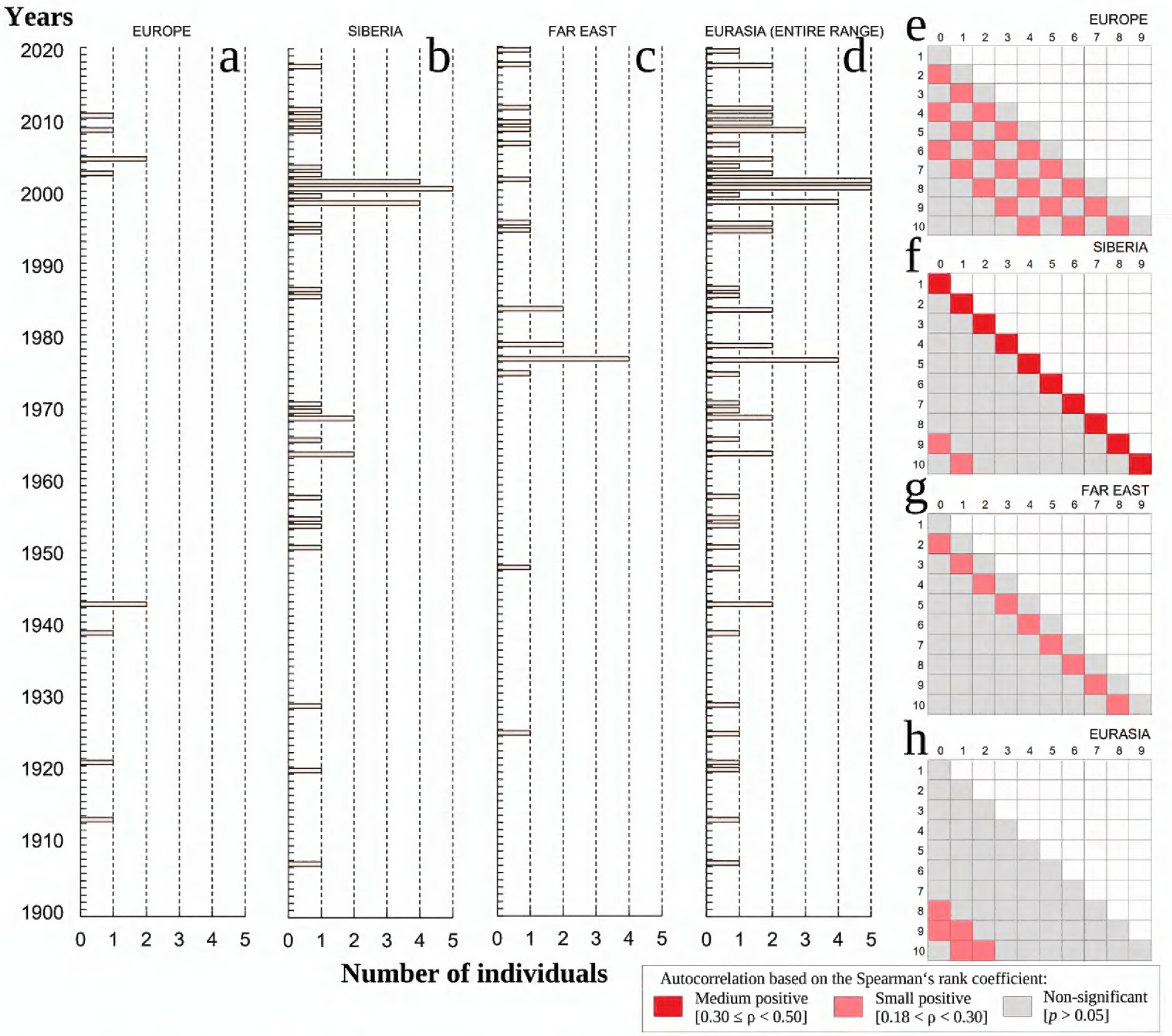

Figure 3. Long-term dynamics of annual captures of *Arctia menetriesii* at the subcontinental and continental scales. **a–d.** Time series of the species' annual captures (imagoes only; 1901–2020): Europe and the Urals ($N = 10$). **a.** Siberia ($n = 39$). **b.** Far East ($n = 20$). **c.** and Eurasia (the entire range; $n = 69$). **d.** The captures without reference to a certain year ($n = 9$) were excluded from the analyses. **e–h.** Autocorrelation maps depicting the Spearman's rank correlation coefficients between the species' annual capture series from the same area with time lag of 0 to 10 years: Europe (**e**); Siberia (**f**); Far East (**g**); and Eurasia (**h**). The numeric values indicate time lag.

The autocorrelation analyses based on Spearman's rank coefficients show that each series of annual captures by region reveals a significant positive autocorrelation signal (Fig. 3e–g). The time series from Europe returns a weak and rather simple autocorrelation pattern with a period of 2, 4, and 6 years (Fig. 3e) due to the odd-year periodical appearance of imago (see below). The Siberian dataset shows a moderate but stable autocorrelation with each previous year for a lag from 1–10 years (Fig. 3f). The time series collected in the Far East reflects a similar stable autocorrelation pattern but with a two-year shift (Fig. 3g). The entire dataset (Eurasia) reveals a weak and highly delayed positive autocorrelation signal with a lag of 8–10 years (Fig. 3h).

Inter-annual capture dynamics of *A. menetriesii* and climate fluctuations

The cross-correlation maps (time lag of 0–10 years) based on the Spearman's rank correlation coefficients between *A. menetriesii* annual captures and climate variables (monthly mean air temperatures, annual mean temperature, and PC1 of monthly mean air temperatures) reveal a significant climatic signal for each of the four datasets, i.e., Europe, Siberia, the Far East, and Eurasia (Fig. 4a–d; Suppl. materials 1–3).

In general, the time series from Europe and Siberia have a rather weak correlation with climate variables, showing a few small negative correlation coefficients (mean temperature of May for Europe and mean temperature of February for Siberia, with a lag of 4 and 0 years, respectively) (Fig. 4a, b). Moreover, the annual capture series from Europe shows small positive correlation with mean temperatures of January (lag = 9 years), July (lag = 6 years), and October (lag = 4 years), as well as with annual mean temperature (lag = 0 years). The time series from Siberia reveals small positive correlation with mean temperatures of March (lag = 10), April (lags = 3 and 5 years), September (lag = 7 years), October (lag = 5 years), as well as with annual mean temperature (lags = 4 and 7 years).

The time series from the Far East reveals moderate positive correlation with mean temperature of May (lag = 0 years) and of June (lag = 4 years), as well as with PC1 of monthly mean air temperatures (lag = 5 years) (Fig. 4c). Furthermore, there are a number of small positive Spearman's correlation coefficients with monthly mean air temperatures (January, March, April, May, June, August, and November), annual mean temperature, and PC1 of monthly mean air temperatures for different lags (Fig. 4c).

The entire (continent-wide) dataset shows a moderate positive climatic signal with monthly mean air temperatures of May (lags = 0 and 5 years), June (lag = 4 years), and December (lag = 7 years), as well as with annual mean temperature and PC1 of monthly mean air temperatures (lags = 4 and 7 years in both cases) (Fig. 4d). Moreover, there are a plethora of small positive correlation coefficients with monthly mean air temperatures (all 12 months), annual mean temperature, and PC1 of monthly mean air temperatures for different lags (Fig. 4d).

Periodical appearance and phenology of *A. menetriesii*

The European imagoes were collected in odd years only (Fig. 2b). Conversely, the numbers of imago collected in odd and even years from Siberia and the Far East do not share significant differences from the equal ratio (Pearson's chi-squared test: $\chi^2 < 0.89$; $df = 1$; $p > 0.271$), although most even-year captures were situated in more southern areas of Asia (Fig. 1a). The median latitude of localities, in which moths were collected in odd years, is significantly higher compared with that of even-year captures (Monte Carlo Randomization test; $p = 0.047$), while

the difference between localities with odd- and even-year appearance of imago by longitude and altitude was non-significant (Monte Carlo Randomization test; $p > 0.245$). Conversely, the results of linear discriminant analyses (LDA) show that 94.6% of localities were correctly assigned to the predicted life cycle (annual vs biennial) based on monthly mean air temperature (Suppl. material 7: table S2).

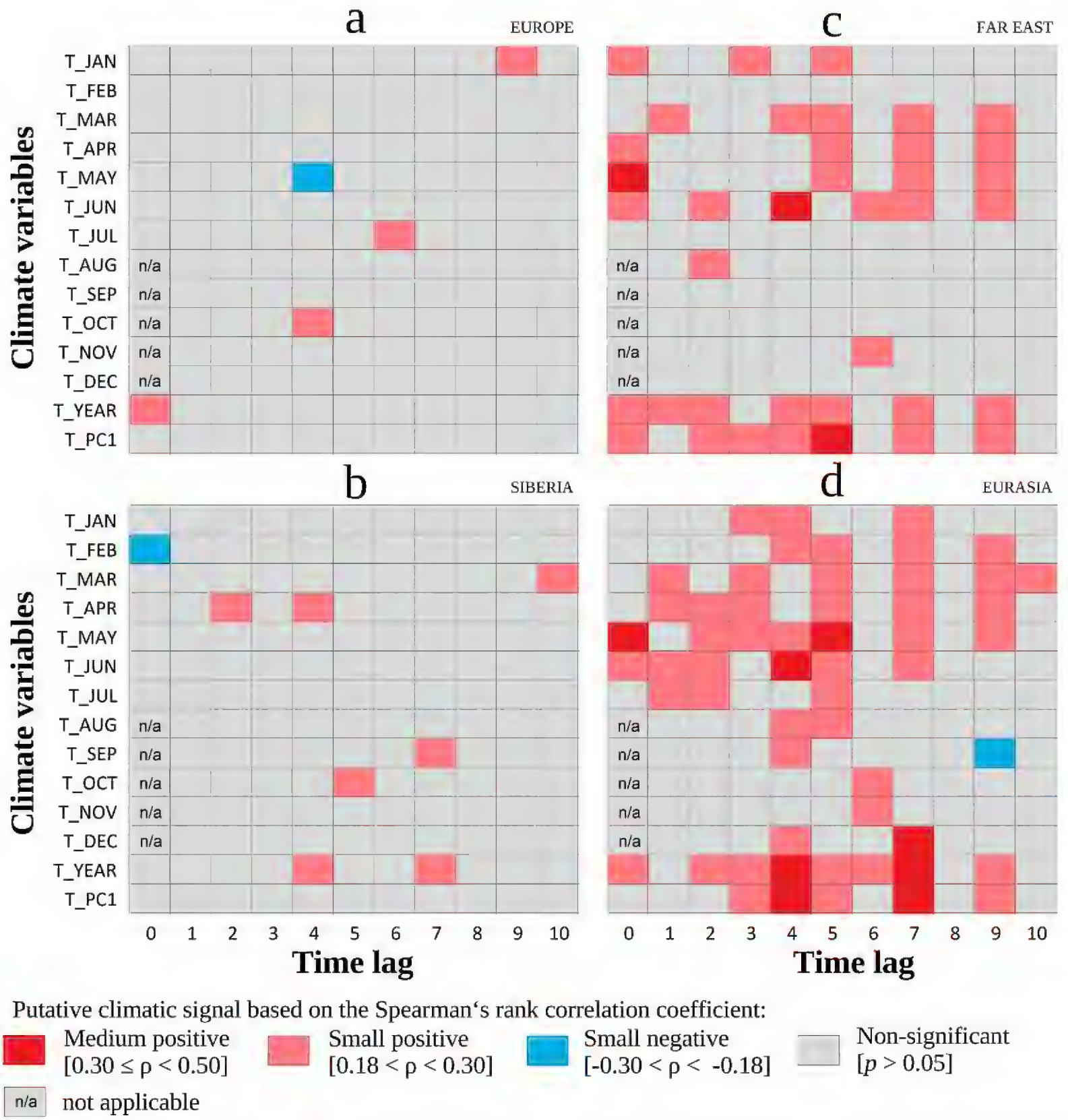

Figure 4. Possible effects of climate fluctuations on the long-term dynamics of annual captures of *Arctia menetriesii*. **a–d.** Cross-correlation maps depicting the Spearman's rank correlation coefficients between the species' annual capture data (time lag of 0 to 10 years) and monthly mean air temperatures (January to December: *T_JAN* … *T_DEC*), annual mean temperature (*T_YEAR*), and PC1 of monthly mean air temperatures (*T_PC1*). **a.** Europe; **b.** Siberia; **c.** Far East; **d.** Eurasia (the entire range). The correlation coefficients and corresponding *p*-values are listed in Suppl. material 2.

Based on the number of imaginal captures by ten-day period, the species shares similar phenological pattern in Europe and Siberia (Pearson's chi-squared test: $\chi^2 = 3.67$; $df = 4$; $p = 0.146$), with the maximum value in the first ten days of July (Fig. 5a, b). In its turn, this pattern in the Far East differs from other regions (Pearson's chi-squared test: $\chi^2 > 11.92$; $df = 4$; $p < 0.008$), with a significant shift of the maximum number of imaginal captures to the second ten-day period of July (Fig. 5c). The shortest flying period is characteristic for European and Far Eastern populations (26 and 28 days, respectively), while in Siberia this period is at least two times longer (52 days). The number of collected females exceeds that of males by 3–7 times in samples from all the regions (Pearson's chi-squared test: $\chi^2 > 5.44$; $df = 1$; $p < 0.020$), while the proportion of individuals, the sex of which was not registered, in the total sample is 18.9% (Fig. 5d). The median data on the flying activity of this species (both sexes) across three regions (Europe, Siberia, and the Far East) is presented in Fig. 5e.

The mean number of eggs (± S.E.) produced by a female was 120 ± 11 (min–max = 105–150; $n = 4$) (Suppl. material 7: table S1). In one case, a prolonged egg-laying period of 10 days (11–20 July 2012) was observed (female ID: AM-035). Other female (AM-066) laid 105 eggs during a day (3 July 2018).

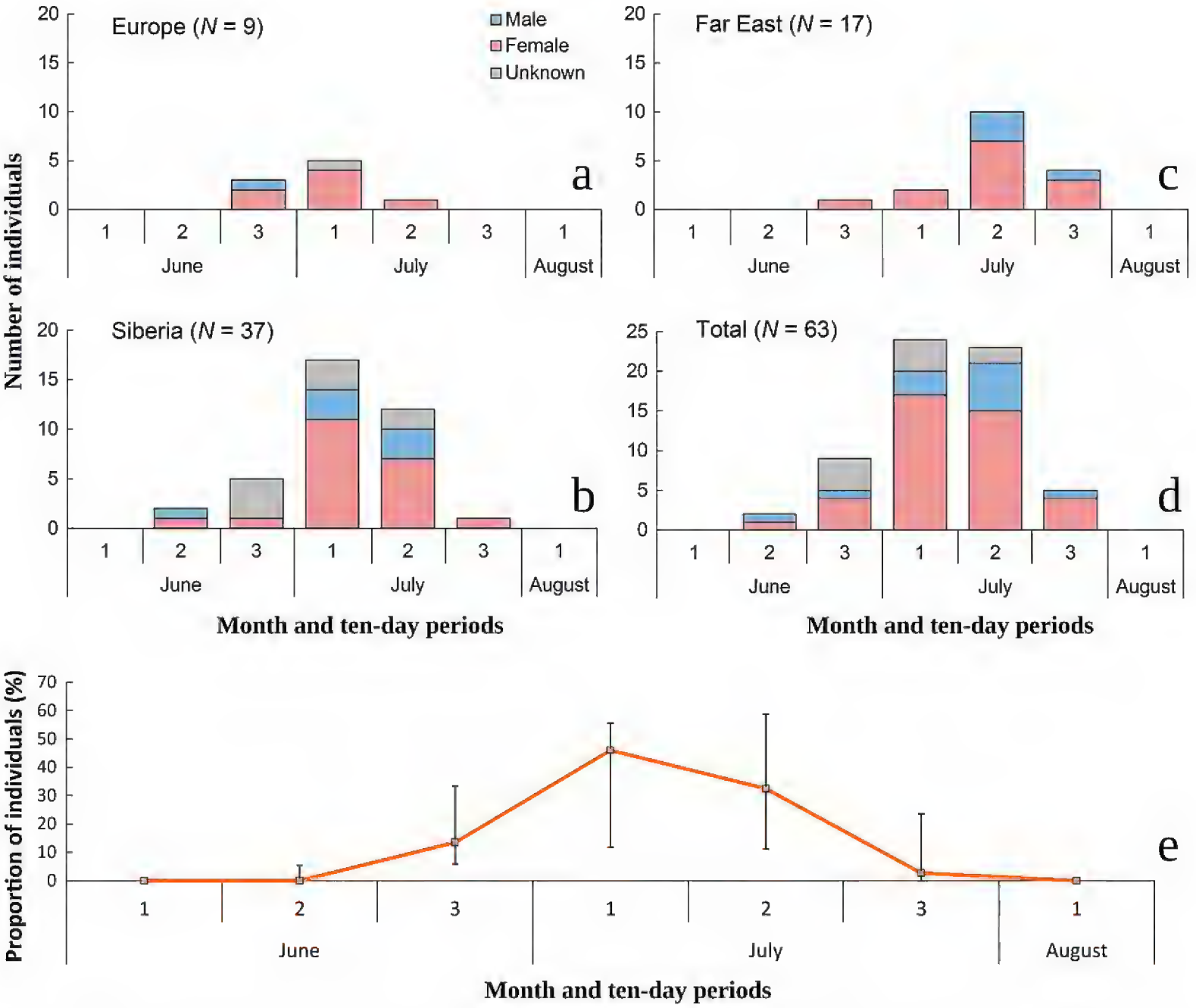

Figure 5. Imaginal phenology of *Arctia menetriesii* at the subcontinental and continental scales. **a.** Europe and the Urals. **b.** Siberia. **c.** Far East. **d.** Eurasia (the entire range). **e.** Median proportion of imago individuals recorded per ten-day period by region ($n = 3$). Error bars indicate standard error estimates based on the bootstrap approach ($B = 1000$ replications).

Environmental preferences of *A. menetriesii*

The results of linear discriminant analyses (LDA) reveal that the species' localities in each region significantly differ by monthly mean air temperature characteristics (Fig. 6a and Suppl. material 1). In total, 98.3% of collecting localities were correctly assigned to certain regions, except for one locality in the Urals (Suppl. material 7: table S3).

Based on the number of imaginal captures by habitat, *A. menetriesii* shares similar environmental preferences in Siberia and the Far East (Pearson's chi-squared test: $\chi^2 = 2.16$; $df = 4$; $p = 0.183$), while its habitat spectrum in Europe strongly differs from those in Asia (Pearson's chi-squared test: $\chi^2 > 2.29$; $df = 4$; $p < 0.001$). In all the regions, the distribution of species captures through habitat patches significantly differs from the discrete uniform distribution (Pearson's chi-squared test: $\chi^2 > 27.63$; $df = 4$; $p < 0.001$), indicating the presence of strong environmental preferences.

Most European records were made in plain coniferous forests of Finland and Russian Karelia (Fig. 6b, c), with two specimens being collected in riparian forests of the Arkhangelsk Oblast and Northern Urals (Fig. 6b–e). In Siberia and the Far East, most specimens were collected in riparian forests (Fig. 6f, g), with a few records from high-altitude environments such as mountain forest (Fig. 6h, i) and open alpine habitats (meadows and tundra), as well as from urban localities. The frequency of species captures in Asian riparian forests and European plain forests significantly higher than that in other kinds of habitats (Pearson's chi-squared test: $\chi^2 > 4.46$; $df = 1$; $p < 0.020$).

A waterbody such as river, stream or lake commonly occurs at the species' collecting localities in Siberia and the Far East (Suppl. material 7: fig. S3). These regions do not share significant differences from each other based on the presence/absence of a waterbody in the sampling sites (Pearson's chi-squared test: $\chi^2 = 3.31$; $df = 1$; $p = 0.069$). In Europe, most samples were collected from plain forest, and this region significantly differs from Siberia (Pearson's chi-squared test: $\chi^2 = 8.61$; $df = 1$; $p = 0.003$) and the Far East (Pearson's chi-squared test: $\chi^2 = 15.10$; $df = 1$; $p < 0.001$) by a general lack of water sources in the species' localities (Suppl. material 7: fig. S3).

Host plant usage, survival patterns, and sex ratios

The larvae of *A. menetriesii* consumed 23 host plant species among 52 plant and one lichen taxa that were tested in laboratory experiments (Table 1 and Suppl. material 4). Two of the confirmed host plants are strongly toxic, that is, *Aconitum rubicundum* and *A. consanguineum* (Ranunculaceae), while nine host plants are weakly toxic: *Comarum palustre* L., *Rubus idaeus* (Rosaceae), *Larix sibirica* Ledeb., *L. cajanderi* Mayr, *L. gmelinii* (Rupr.) Kuzen (Pinaceae), *Menyanthes trifoliata* L. (Menyanthaceae), *Persicaria lapathifolia* (L.) Delarbre, *Rumex crispus* L. (Polygonaceae), and *Vaccinium uliginosum* L. (Ericaceae).

E. S. Koshkin's breeding experiment without hibernation (offspring of the female AM-066, Russian Far East) indicates that larvae readily feed on *Aconitum consanguineum* but the presence of this strongly toxic plant in larval diet significantly decreases the survival of preimaginal stages based on Kaplan-Meier estimator (Wilcoxon test: $P = 0.0273$) (Fig. 7a and Suppl. material 5; see also Suppl. material 7: note S1). Moreover, larval feeding on alkaloid-rich *Aconitum* leaves leads to various metamorphosis anomalies such as larva-pupa intermediate and imago with undeveloped wings (Suppl. material 5).

The total mortality rate of the species recovered from a series of breeding experiments was very high (mean ± S.E. = 89.8 ± 4.3%, min–max = 71.8–100%, $n = 7$) (Suppl. material 7: table S1). The Kaplan-Meier survival plot based on the combined data from breeding experiments with hibernation reveals that the maximum mortality did occur at larval stage during the hibernation period (Fig. 7b–e) due to an unidentified fungal disease, freezing caused by hard winter frosts with

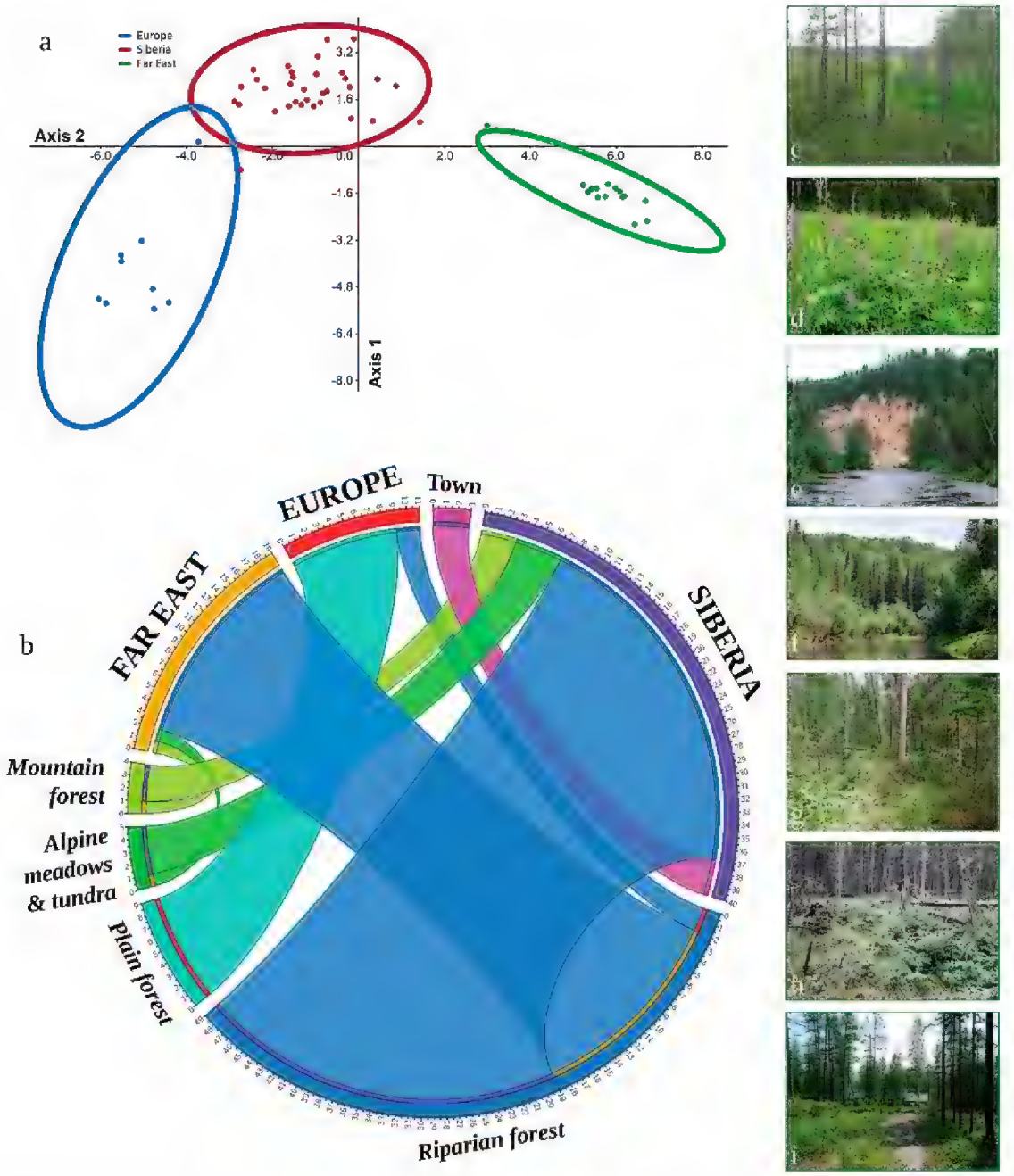

Figure 6. Climatic niche and habitat breadth of *Arctia menetriesii* in different parts of the range. **a.** Discriminant analysis of localities by region on monthly mean air temperature characteristics. Axes 1 and 2 explain 71.2% and 28.8% of the total variation, respectively. **b.** Circos plot showing the habitat breadth of the species based on the number of imaginal and larval samples categorized by region. The scales represent the number of collected specimens. Regions are represented by arcs on the left half of the circle with a length determined by the number of specimens: Europe (red); Siberia (violet); and Far East (light brown). Linking lines between regions represent shared habitats, with the thickness proportional to the number of collected specimens for each type of habitat; line colour refers to the type of habitat, while narrow colour arcs inserted near the top of linking lines refer to the number of samples by region. The plot was created using the online application of Circos (http://mkweb.bcgsc.ca/tableviewer) (Krzywinski et al. 2009). **c–i.** Examples of habitat photos: **c.** Half-open bog surrounded by pine and spruce forest, Finland (habitat category: plain forest; occurrence IDs: AM-006 and AM-007). **d.** Humid mixed-herb meadow surrounded by Siberian spruce and Siberian larch forest, Sotka River valley, Pinega State Nature Reserve, European Russia (habitat category: riparian forest; occurrence ID: AM-010). **e.** Gypsum outcrop with perennial cave ice at the same site. **f.** Mixed taiga forest, Negusyakh River valley, Yugansky State Nature Reserve, Siberia, Russia (habitat category: riparian forest; occurrence IDs: AM-014, AM-015, and AM-016). **g.** Mixed coniferous taiga forest, Bolshoy Anay River valley, Baikalo-Lensky Nature Reserve, Siberia, Russia (habitat category: riparian forest; occurrence ID: AM-030). **h.** Cedar and fir forest with *Aconitum* spp. and other tall herbs on a mountain slope, Chikoy National Park, Siberia, Russia (habitat category: mountain forest; occurrence ID: AM-042). **i.** Larch forest, upstream of the Pravaya Bureya River, near cordon "Novy Medvezhii", Bureya State Nature Reserve, Russian Far East (habitat category: mountain forest; occurrence ID: AM-066). Photos: Risto Haverinen (**c**); Yulia S. Kolosova (**d, e**); Evgeny G. Strelnikov (**f**); Oleg E. Berlov (**g**); Pekka Alestalo (**h**); and Evgeny S. Koshkin (**i**).

Table 1. Host plants of *Arctia menetriesii* based on experimental and field observation data (Suppl. material 4).

Plant species	Plant family	Origin	Plant species toxicity*	Type of data
Taraxacum officinale (L.) Weber ex Wigg.	Asteraceae	Native	Nontoxic	Laboratory experiment
Vaccinium uliginosum L.	Ericaceae	Native	Weakly toxic	Laboratory experiment
Ribes nigrum L.**	Grossulariaceae	Native	Nontoxic	Laboratory experiment
Ribes rubrum L.**	Grossulariaceae	Native	Nontoxic	Laboratory experiment
Menyanthes trifoliata L.	Menyanthaceae	Native	Weakly toxic	Laboratory experiment
Larix sibirica Ledeb.	Pinaceae	Native	Weakly toxic	Laboratory experiment
Larix cajanderi Mayr.	Pinaceae	Native	Weakly toxic	Laboratory experiment
Larix gmelinii (Rupr.) Rupr.	Pinaceae	Native	Weakly toxic	Laboratory experiment
Plantago major L.	Plantaginaceae	Native	Nontoxic	Laboratory experiment
Persicaria maculosa Gray	Polygonaceae	Native	Nontoxic	Laboratory experiment
Persicaria lapathifolia (L.) Delarbre	Polygonaceae	Native	Weakly toxic	Laboratory experiment
Rumex crispus L.	Polygonaceae	Native	Weakly toxic	Laboratory experiment
Aconitum rubicundum Fischer	Ranunculaceae	Native	Strongly toxic	Field observations
Aconitum consanguineum Vorosch.	Ranunculaceae	Native	Strongly toxic	Laboratory experiment
Comarum palustre L.	Rosaceae	Native	Weakly toxic	Laboratory experiment
Fragaria × *ananassa* (Duchesne ex Weston) Duchesne ex Rozier**	Rosaceae	Non-native	Nontoxic	Laboratory experiment
Malus baccata (L.) Borkh.	Rosaceae	Native	Nontoxic	Laboratory experiment
Prunus domestica L.	Rosaceae	Native	Nontoxic	Laboratory experiment
Rubus chamaemorus L.	Rosaceae	Native	Nontoxic	Laboratory experiment
Rubus idaeus L.	Rosaceae	Native	Weakly toxic	Laboratory experiment
Rubus saxatilis L.	Rosaceae	Native	Nontoxic	Laboratory experiment
Salix phylicifolia L.**	Salicaceae	Native	Nontoxic	Laboratory experiment
Viola riviniana Rchb.	Violaceae	Native	Nontoxic	Laboratory experiment

*Toxicity estimates are based on published sources (Manoliu 1975; Titovich et al. 2009; Kubinova et al. 2014; Jansone et al. 2017; Günthardt et al. 2018; Sepahvand et al. 2021; The PLANTS Database 2021).
**Cultivated plants.

extremely low temperatures, and desiccation (see Suppl. material 7: table S1, note S1 and Suppl. material 6 for detail). Based on experimental data, the mean larval mortality (± S.E.) was 84.6 ± 6.2% (min–max = 56–100%, $n = 7$).

The sex ratio of *A. menetriesii* in the four successful breeding experiments was balanced (Pearson's chi-squared test: $\chi^2 < 1.14$; $df = 1$; $p > 0.285$), with a slight prevalence of males in some cases (Fig. 7f and Suppl. material 7: table S1). Conversely, the samples collected from natural environments produced a strongly female-biased sex ratio, which ranges from 0.13 to 0.35 in different regions and shows significant differences from the equal ratio (see above).

Discussion

Is *A. menetriesii* characterized by exceptional rarity or low detectability?

Our results reveal that *A. menetriesii* possesses the following ecological traits: (1) a vast distributional range; (2) a rather wide range of habitats (from various types of forests to alpine meadows); (3) the lack of a clear host-plant specialization; and (4) the extremely low number of records (< 100 specimens per ca. 170 years). It is well-known that rare moth and butterfly species may be abundant locally in a specific habitat (e.g. Bolotov et al. 2013c; New 2023) but *A. menetriesii* was

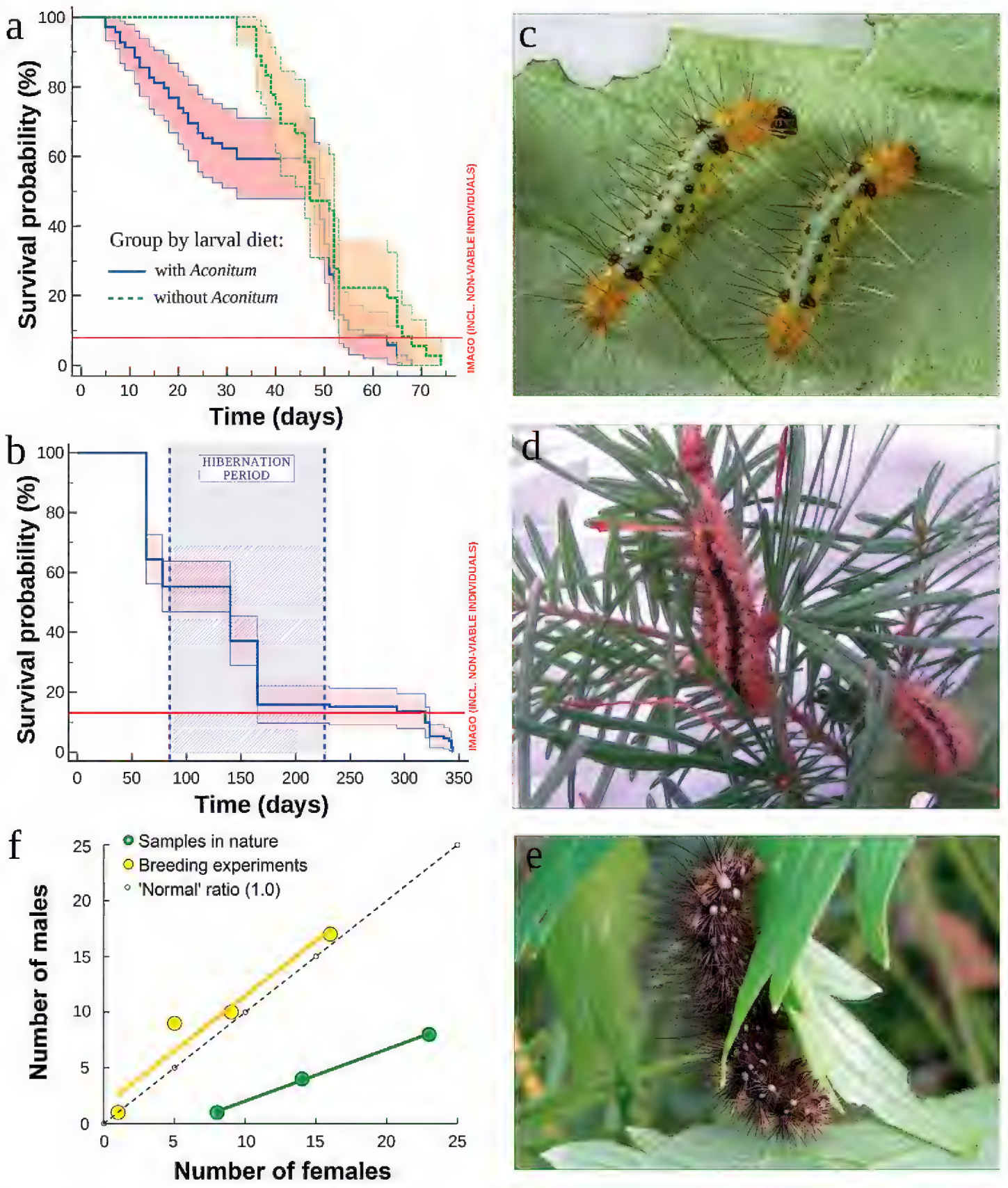

Figure 7. Survival rates, sex ratio, and images of living larvae on host plants of *Arctia menetriesii*. **a.** Kaplan-Meier survival plot based on the data obtained from E. S. Koshkin's breeding experiment without hibernation: offspring of the female AM-066, Russian Far East. Coloured areas indicate 95% confidence intervals for each survival curve. The original data is given in Suppl. material 5. **b.** Kaplan-Meier survival plot based on the data obtained from breeding experiments of H. Krogerus and H. Saarenmaa et al. with hibernation: offspring of the females AM-002 from Finland and AM-037 from Eastern Siberia, respectively. Coloured area indicates 95% confidence interval of the survival curve. The original data is given in Suppl. material 6. **c.** Reared 2nd instar larvae on a leaf of *Aconitum consanguineum*: offspring of the female AM-066. **d.** Reared 6th instar larva on *Larix sibirica*, showing larval camouflage pattern: offspring of the female AM-037. **e.** Native last (7th) instar larva feeding on *Aconitum rubicundum*, Eastern Siberia (occurrence ID: AM-030). **f.** Sex ratio in field samples (Europe, Siberia, and the Far East) and breeding experiments (see Suppl. material 7: table S1 for detail). The black dashed line shows a hypothetical optimal ratio (1:1). Photos: Evgeny S. Koshkin (**c**); Hannu Saarenmaa (**d**); and Oleg E. Berlov (**e**).

never found as common in any locality and any type of habitat during over a century-long period of observations (Bolotov et al. 2022a). At first glance, the constantly low number of records argues in favor of the extreme rarity of this species due to some natural reasons (Krogerus 1944; Kaisila 1947; Bolotov et al. 2013a; Saarenmaa 2021; Bolotov et al. 2022a). This hypothesis presumes that *A. menetriesii* has extremely small population sizes over its trans-continental range but it is unclear how an insect species may continually reproduce and disperse at such a low density of individuals.

Conversely, the extremely low number of available records may also be explained by the low detectability of *A. menetriesii* in nature. The low detectability could be associated with its preference to hard-to-reach, unpopulated areas (e.g., primeval taiga forests in river valleys and high-elevation meadows), short flight period of imago, and, perhaps, to reduced daily activity (crepuscular adult moths and nocturnal larvae). It is well-known that many moth species described from more remote parts of the world are still known by a few type specimens due to the scarcity of sampling efforts (New 2023). In the case of *A. menetriesii*, the difference between a strongly female-biased sex ratio in field samples and a balanced (equal) sex ratio in breeding experiments may indicate that the low detectability plays a significant role in the low number of observations and that by some reasons males are harder to find in the field compared with females. Moreover, light traps and pheromone attractants seem to be ineffective for this species (Tähtinen 2015), although at least two specimens were collected near light sources (Bolotov et al. 2022b).

Available information on the ecological and biological traits of *A. menetriesii* is too limited to estimate a contribution of each of the two possible causes in the general rarity of the species. In our opinion, the low number of the species' records results from the combined influence of both possible causes, i.e., the inconspicuous lifestyle and low natural population abundance (at least on the imaginal stage – see below). For instance, *Arctia tundrana* (Tshistjakov, 1990), another example of 'extremely rare' moth, can be abundant locally at the larval stage but records of its imagoes are scarce (only 35 localities in northern Eurasia during the period of 1904–2019) due to the high mortality of larvae after parasitoid pressure and the species' confinement to remote, uninhabited Arctic areas (Bolotov et al. 2015; Bolotov et al. 2021).

Potential limiting factors that may contribute to the rarity of *A. menetriesii*

Here, we show that the inter-annual capture dynamics of *A. menetriesii* may partly be explained by climate (air temperature) influence. In most cases, we recorded positive Spearman's correlation coefficients between annual captures and temperature characteristics with temporal lag of 0 to 10 years, indicating that colder weather conditions in current and previous years may decrease the abundance of the species. In some cases, we also discovered small negative correlation coefficients with mean temperature of May (Europe), February (Siberia), and September (Eurasia), probably indicating the adverse impact of freeze/thaw events on larvae (Bolotov et al. 2013b). Experimental data indicate that the highest mortality rate does occur in overwintering larvae due to either fungal disease or extreme cold events (winter hard frosts) (Suppl. material 7: tables S1, S4). Additionally, experimental observations suggest that desiccation-driven mortality during hibernation period may also contribute to the lowered larval survival rate (Suppl. material 7: note S1). Field observations show that short-term summer cold events (i.e., summer frosts) may negatively affect the abundance of imago, especially in mountain areas (Suppl. material 7: table S4 and Fig. 8). Conversely, temperature in the species' microhabitats may differ from air temperature estimates (Scheffers et al. 2014), especially in karst areas with perennial cave ice (Bolotov et al. 2013a; also see Fig. 6e).

We show that larvae of *A. menetriesii* feeding on *Aconitum* leaves in a laboratory experiment are characterized by much higher mortality rates compared with those feeding on non-toxic or weakly toxic plants (see Fig. 7a). Moreover, specific metamorphosis anomalies and wing development defects frequently occurred when larvae used *Aconitum* leaves in their experimental diet (Koshkin 2021). Similar metamorphosis anomalies were recorded in experimental populations of other moth species feeding on toxic plants (Mason et al. 2014). One case of wing development defects was discovered in a wild female from the Northern Urals (occurrence ID: AM-011) (Ermakov 2006; Nupponen and Fibiger 2012; Bolotov et al. 2022a; Bolotov et al. 2022b), while native larvae were recorded feeding on *Aconitum rubicundum* in Eastern Siberia (occurrence ID: AM-030) (Berlov and Bolotov 2015; Bolotov et al. 2022a; Bolotov et al. 2022b). These data indicate that larvae of *A. menetriesii* may use toxic host plants in nature and that this tendency could also contribute to the extreme rarity of this species (see Fig. 8). Multiple Lepidoptera species are known to feed on toxic plants to selectively utilize (sequestrate) various plant compounds (e.g., pyrrolizidine alkaloids) that are used in physiological and biochemical mechanisms such as chemical defense and sexual behavior (Schulz 1998; Nishida 2002; Martins and Trigo 2016). For example, the production of pheromones by adult moths may depend on the consumption of plant secondary metabolites by larvae (von Nickisch-Rosenegk and Wink 1993; Schulz 1998; Wink 2018). It was assumed that the failure of female tiger moths (*Phragmatobia* spp.) to detect the display of alkaloid-derived pheromone may be linked to an evolutionary shift from an ancestral larval host range restricted to toxic plants containing pyrrolizidine alkaloids to the polyphagy (Krasnoff and Roelofs 1990). We assume that feeding of *A. menetriesii* on toxic host plants such as *Aconitum* spp. may serve as a self-defense mechanism against fungal disease, which infects the hibernating larvae, by uptake of plant toxins. If so, the choice between toxic and non-toxic host plants may come with a trade-off between negative (decreased survival and metamorphosis anomalies) and positive (defense from fungi and other pathogens) effects of toxin uptake (Dickel 2018). However, this preliminary hypothesis needs to be tested experimentally in the future.

Another enigmatic feature of this species is a strong female-biased sex ratio in the field samples. Our data indicates that it is not a natural phenomenon but a potential sampling artifact, because sex ratio in experimental brood was close to 1.0. It is known that differences in each sex proportion recorded in field samples/observations do not uncover the actual sex ratio of a given species but, in many cases, reflect behavioral differences between males and females (Ellis et al. 2022). In particular, male-biased sex ratios commonly occur in field samples of Lepidoptera due to the higher activity of males (Beck et al. 2006; Altermatt et al. 2009; Gorbach 2018; Brehm et al. 2019; Nino et al. 2019; Ellis et al. 2022). Conversely, a specific larval diet may support the development of males (Quezada-Garcia et al. 2014), while the prevalence of females could be linked to parthenogenesis (Schmidt and De Freina 2011) and the influence of *Wolbachia* endosymbionts, selectively eliminating males (Brehm et al. 2019). Either way, specific reasons that may cause female-biased sex ratio in field samples of *A. menetriesii* are yet to be understood, although the lower detectability of males seems to be the most likely cause.

In summary, our analyses indicate that the long-term series of *A. menetriesii* annual captures in Europe and Asia may reflect natural population dynamics, influenced by climatic (air temperature) fluctuations, and, perhaps, some additional environmental factors and life history traits. This pattern does not correspond to the global trend of declines in insect abundance during the last decades that

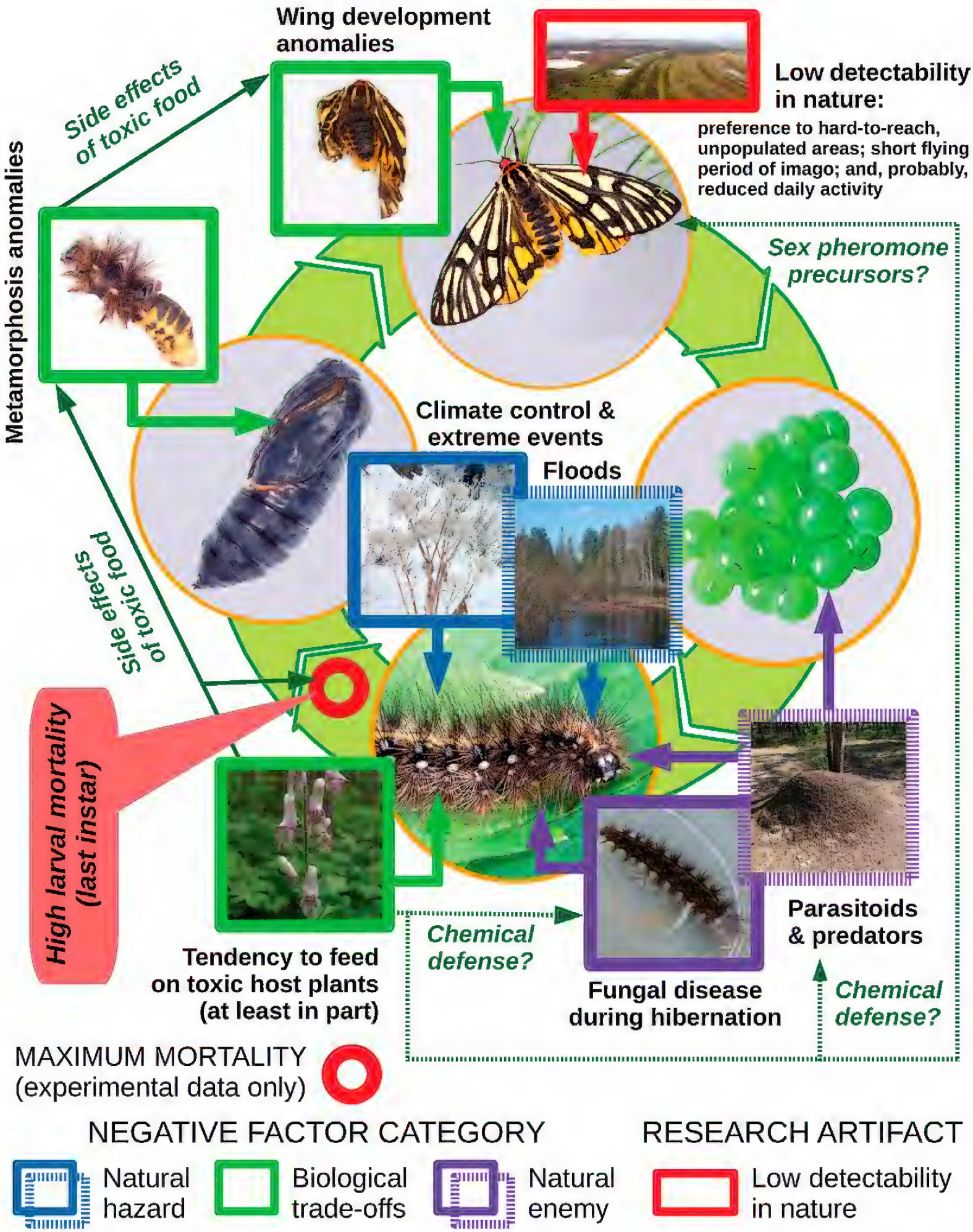
Wing development anomalies
Side effects of toxic food
Low detectability in nature:
preference to hard-to-reach, unpopulated areas; short flying period of imago; and, probably, reduced daily activity
Metamorphosis anomalies
Sex pheromone precursors?
Climate control & extreme events
Floods
Side effects of toxic food
High larval mortality (last instar)
Tendency to feed on toxic host plants (at least in part)
Chemical defense?
Fungal disease during hibernation
Parasitoids & predators
Chemical defense?
MAXIMUM MORTALITY (experimental data only)
NEGATIVE FACTOR CATEGORY
Natural hazard
Biological trade-offs
Natural enemy
RESEARCH ARTIFACT
Low detectability in nature

Figure 8. Hypothetical scheme, showing potential factors and causes, which may contribute to the 'exceptional rarity' and/or low detectability of *Arctia menetriesii* at different stages of its life cycle. Solid frames indicate confirmed factors/causes, and dashed frames indicate factors/causes proposed on the basis of indirect evidence. Potential factors and causes are explained in Suppl. material 7: table S4. Photos: Oleg E. Berlov, Evgeny S. Koshkin, Kimmo Silvonen, Yulia S. Kolosova, and Ivan N. Bolotov.

was recovered in a large body of literature (Goulson 2019; Van Klink et al. 2020; Finn et al. 2023). However, it was shown that different insect species (and moths in particular) exhibit different population trajectories (Kozlov et al. 2006; Crossley et al. 2020; Wagner et al. 2021), with steeper declines in host specialists, as well as in darker-coloured and larger-sized moths (Coulthard et al. 2019; Roth et al. 2021; Blumgart et al. 2022). Moreover, most striking examples of insect declines are confined to densely populated areas of Europe and North America, characterizing by intensive agriculture, wide usage of pesticides, high urbanization rate, and deterioration of habitat qualities (Hallmann et al. 2017; Habel et al. 2019; Wagner 2020; Habel et al. 2022). In turn, *A. menetriesii* exclusively inhabits primeval taiga forests, whose massive and high quality patches still do remain in Northern Eurasia.

There are some additional factors that may greatly decrease the abundance of *A. menetriesii*, although we do not have direct evidence, supporting their significance (see Fig. 8 and Suppl. material 7: table S4 for detail). In particular, parasitoid pressure may cause a high mortality rate in Lepidoptera species (Hammami et al. 2023). It was shown experimentally that 90.8% of *Arctia tundrana* last instar larvae from Northern European Russia died due to infestation by *Meteorus* sp. (Hymenoptera: Braconidae) (Bolotov et al. 2015). High mortality rates (approximately 50%) were also recorded in *Spiris bipunctata* (Staudinger, 1892) from Eastern Siberia due to tachinid fly (Diptera: Tachinidae) infestation (Shilenkov and Richter 1998). Larval parasitism is an important source of mortality in butterflies but its rate varies along environmental gradients (Stefanescu et al. 2022). These data indicate that larval parasitism should also contribute to the rarity of *A. menetriesii* but the mortality rate caused by this factor is yet to be estimated. Next, *A. menetriesii* populations may also be affected by predator pressure (e.g., by ants and spiders), as shown for other tiger moth species (Mason et al. 2014). Finally, *A. menetriesii* most frequently occurs near rivers and streams, and hence, its larvae could negatively be influenced by seasonal and extreme flood events (Harvey et al. 2023). There are documented examples when seasonal flooding caused high mortality in overwintering larvae and pupae of Lepidoptera (Nicholls and Pullin 2003; Kulak 2024).

Habitat preferences of *A. menetriesii*

Our results based on nearly all captures of *A. menetriesii* available to date (Bolotov et al. 2022a; Bolotov et al. 2022b) reveal that in Siberia and the Far East this species clearly prefers riparian (mostly coniferous) forests. In these regions, most specimens were collected close to a waterbody, i.e. in river and stream valleys, as well as on lake shores. There are a few samples from high-elevation mountain ranges up to 1540–1740 m, some of which were also collected from sites situated not so far from a stream or a river. Three records from urban sites (city of Krasnoyarsk and settlements of Sukhoy Ruchey and Onokhoy) could be linked to vagrant specimens, which come from surrounding natural habitats.

The habitat preference of *A. menetriesii* in Europe shifts to plain coniferous forests. In particular, all the westernmost occurrences in Europe (Finland) come from this type of habitats (often connected with half-open bogs). Specimens from Eastern Europe (Arkhangelsk Oblast of Russia) and the Urals (Sverdlovsk Oblast of Russia) were collected in riparian forests. It is clear that the Finnish population is characterized by a specific habitat preference compared with those in other parts of the species range. The unique record from Eastern Europe (Arkhangelsk Oblast) is somewhat remarkable, because that specimen was collected in karst landscape with multiple gypsum and anhydrite rock outcrops, deeply incised ravines and river valleys, and massive perennial cave ice, supporting cold microclimate (Bolotov et al. 2013a).

In summary, most habitats of *A. menetriesii* are associated with primeval coniferous taiga forests. Usually, the species prefers humid sites in river/stream valleys, on lake shores (Asia), and near peat bogs (Europe). Available records in urban localities could indicate that some adults are able to migrate, at least over short distances of 5–20 km. A few findings from the top of high mountains may suggest occasional vertical dispersal or, alternatively, may indicate the presence of specific high-altitude populations, inhabiting open alpine environments. The most northern record in the Muksunuokha River valley (Yana-Indigirka Lowland; 71.9°N) could indeed be associated with riparian forest patches (Bolotov et al. 2013a).

We discovered an exponential latitudinal shift in *A. menetriesii* occurrences from plain to highland localities in the southern direction, with the lowest and highest points being the northern and southern extremities of the range, respectively (see Fig. 2d). This pattern could also be explained by environmental preferences of the species, as coniferous forests shift to mountain belts in more southern areas (Nakamura and Krestov 2005; Zhang et al. 2021). Moreover, multiple northern animal and plant species are known to occupy southern mountain areas (Makhrov et al. 2019). Three records from the Suntar-Khayata Mountains in Yakutia represent an exception from the general pattern and may belong to a cold-adapted intraspecific lineage. The unique record from a plain coastal area of the Okhotsk Sea is also rather unusual but that moth has probably arrived from nearby hills (alt. 450–550 m), because the distance between its collecting site and the hill ridge is 1.5–2 km only.

Our findings align with earlier hypotheses on a relative 'continentality' of *A. menetriesii* and its strong preference to the 'Siberian-type' taiga landscapes and primeval coniferous forests (Filipiev 1916; Krogerus 1944; Kaisila 1947; Bolotov et al. 2013a; Berlov and Bolotov 2015; Bolotov et al. 2022a). Several other insect species such as the Eurasian taiga bumblebees *Bombus consobrinus* Dahlbom 1832, *B. patagiatus* Nylander, 1848, *B. schrencki* Morawitz, 1881, and *B. semenoviellus* Skorikov, 1910 reveal similar environmental preferences and distribution patterns (Løken 1973; Bolotov and Kolosova 2006; Rasmont and Iserbyt 2014; Potapov and Kolosova 2021).

Inter-population differences of *A. menetriesii* in Europe and Asia

The population of *A. menetriesii* in Europe differs from those in Asia in several ways. First, in Europe it occurs far more rarely and much more scarcely. Second, all the European imagoes were recorded in odd years (exclusively biennial life cycle), while there are no significant differences between the number of imaginal records in even and odd years in Siberia and the Far East. Third, all the European localities are situated within narrow elevational and latitudinal ranges and are confined to non-mountainous sites. Fourth, in Europe it exhibits much narrower habitat breadth compared with that in the Asian part of the range. Fifth, in Finland it is confined to rather specific habitats (plain forests, often with half-open peat bogs), which differ from those in other parts of the continent. Sixth, its flying period in Europe is two times shorter than that in Siberia, though it is comparable with that in the Far East.

At first glance, these differences could reflect the founder effect. The population in Europe (or at least that in Finland) should have had a postglacial allochthonous origin, because this area was completely covered by a massive ice sheet during the Last Glacial Maximum (Hewitt 1999; Mangerud et al. 2002; Svendsen et al. 2004; Lambeck et al. 2010). Based on available data inferred from other boreal and Arctic-alpine species of animals and plants (Makhrov and Bolotov 2006; Skrede et al. 2006; Tollefsrud et al. 2008; Tollefsrud et al. 2009; Hantemirova et al. 2017), we could assume that the European population was originated through a dispersal event from a glacial refugium in the Russian

Plain, the Ural Mountains or Siberia. In this case, migrants probably belonged to a single phylogenetic lineage preferring a coniferous forest – peat bog ecotone as habitat and having a biennial development (odd-year cohort), as it has been hypothesized for *Xestia* moths (Noctuidae) and *Erebia* butterflies (Nymphalidae) (Mikkola and Kononenko 1989; Kleckova et al. 2015). This assumption could be checked in the future by means of a phylogeographic approach using microsatellite markers. However, collecting a sufficient amount of fresh material for such a survey appears to be next to impossible, at least from Europe, due to the extreme rarity and/or low detectability of this species.

Another possible explanation is that environmental conditions of the European subcontinent as a whole and Scandinavia in particular are largely unfavorable for a 'continental' species such as *A. menetriesii*. This hypothesis predicts that the species' existence near the limits of its tolerance to one or several ecological factors may trigger significant deviations in its ecology and life history, e.g. the limited habitat breadth and shift to a rather unusual environment, biennial life cycle (alternate-year appearance), reduced seasonal period of imaginal activity, and decreased population abundance. Such deviations commonly occur in peripheral populations of insects, including moths, butterflies, and ground beetles, inhabiting high-latitude and high-elevation areas with extreme environmental conditions (Sota 1996; Sharova and Khobrakova 2005; Filippov 2006; Bolotov et al. 2013c; Ravenscroft 2021). Our analyses reveal that Asian localities, sharing odd-year appearance of *A. menetriesii* imago, are confined to higher-latitude areas, supporting the hypothesis on a potential shift from annual to biennial development in colder climate conditions.

In summary, the spatial patterns and shifts of *A. menetriesii* life cycle in the wild are still poorly understood. Theoretically, this species may maintain either a constant biennial development throughout the entire range with partial coexistence of two alternate-year, more or less reproductively isolated cohorts (Nice and Shapiro 2001; Kleckova et al. 2015) or a variable life cycle shifting between annual and biennial phases depending on the environmental conditions and climatic fluctuations (Vila and Björklund 2004). Alternatively, there is a possibility of asynchronous larval development within a single population, when a part of larvae may have a prolonged biennial development, while the rest of larvae develop during one year (Ravenscroft 2021). A temperature-dependent asynchronous development of insects may also occur in different mountain belts, with altitudinal shift from univoltine to two-year reproduction (Hodkinson 2005).

Conclusions

Menetries' Tiger Moth *Arctia menetriesii* is famous among the global community of researchers, amateur collectors, and nature lovers for its exceptional rarity, large size, and bright colouration. Most available specimens of this species were collected occasionally, while systematically designed long-term research efforts in Europe, Siberia, and the Far East were hardly successful (Bolotov et al. 2013a; Tähtinen 2015; Koshkin 2021; Bolotov et al. 2022a). Generally, the low number of specimen records is the most enigmatic feature of this species (Krogerus 1944; Bolotov et al. 2013a; Bolotov et al. 2022a).

Here, we analyze all available information on ecological, biological, and life-history traits of *A. menetriesii* using a set of statistical approaches. New findings of this study in comparison with earlier sources (Krogerus 1944; Bolotov et al. 2013a; Berlov and Bolotov 2015; Tähtinen 2015; Koshkin 2021; Saarenmaa 2021; Bolotov et al. 2022a) are as follows. First, we show that there is a shift from plain to mountain localities in southern direction that may be explained by a similar

displacement of its preferred habitats such as coniferous forests and humid tall-herb meadows. Second, the long-term series of annual captures by region are characterized by clear autocorrelation patterns that could partly be attributed to periodical appearance of imago. Third, the inter-annual capture dynamics in three regions (Europe, Siberia, and the Far East) and in the entire range seem to be driven, at least in part, by air temperature fluctuations, where warmer weather conditions in the current and past years positively influence the number of sampled imagoes. Fourth, the median latitude of localities with odd-year appearance of imago was higher compared with that of sites with even-year appearance, probably indicating latitudinal shifts in the life cycle. Fifth, regional phenological patterns were illustrated and the frequent presence of a waterbody in the collecting localities was shown. Sixth, a summary from breeding experiments indicates that the highest mortality occurs at the larval stage and that feeding on strongly toxic host plants (*Aconitum* spp.) significantly decreases the survival rate of the species. Seventh, natural samples of *A. menetriesii* have a strongly female-biased sex ratio, while breeding experiments return an equal proportion between females and males. Last but not least, the ecological and life-history differences between European and Asian populations were summarized and discussed for the first time.

As a visual summary, we here propose a hypothetical scheme, showing potential factors and causes, which, in our opinion, may contribute to the 'exceptional rarity' and/or low detectability of *A. menetriesii* (Fig. 8 and Suppl. material 7: table S4). The low number of collected specimens of this species may be a research artifact, reflecting its low detectability in nature due to preference to uninhabited, poorly accessible areas and an inconspicuous lifestyle, as it was noted above. In turn, potential limiting factors could be delineated to natural hazards (climate fluctuations, extreme climate events, and floods), natural enemies (fungal diseases, parasitoids and predators), and biological trade-offs (presence of toxic host plants in larval diet) (Fig. 8 and Suppl. material 7: table S4).

Our non-parametric correlation analyses suggest that the long-term dynamics of *A. menetriesii* annual captures could partly be explained by climate (air temperature) fluctuations, although it is unclear whether even a long-term series of occasional specimen records may correctly reflect the natural population dynamics of this species. Extreme events such as the extremely low temperatures in winter, summer frosts, and floods (especially in narrow river valleys) may decrease the population abundance of *A. menetriesii* at local and regional spatial scales. Natural enemies affecting populations of *A. menetriesii* are almost unknown, although data from experiments reveal that in several cases hibernating larvae were lost due to an unidentified fungal disease. Based on information for other species, we could assume that parasitoids and, to a lesser degree, predators may strongly influence the species' abundance.

Next, larvae of *A. menetriesii* were recorded feeding on strongly toxic host plants (*Aconitum*) under both natural and laboratory conditions (Berlov and Bolotov 2015; Koshkin 2021). A wild last-instar larva from Eastern Siberia consumed only leaves of *Aconitum rubicundum* and did not accept other host plants, including dandelion (*Taraxacum* sp.) and plantain (*Plantago* sp.) leaves (Berlov and Bolotov 2015). Reared larvae from the Far East consumed leaves of *Aconitum consanguineum* but exhibit various developmental anomalies and increased mortality (Koshkin 2021). We assume that selective consumption of toxic plants by larvae is a trade-off between the need to alkaloid uptake (e.g. as potential precursors for pheromone and chemical defense mechanisms; Nishida 2002) and the negative side effects of toxic food.

We hope that our hypothetical scheme with potential factors and causes that may contribute to the low number of *A. menetriesii* records (Fig. 8) could serve as a basic proposal for choosing the

directions of future studies of this iconic species, including search for wild larvae to estimate the infestation level by parasitoids. However, the exceptional rarity (or low detectability) hampers any systematic research focused on this species, because even long-term and broad searching efforts may not be successful (e.g. Tähtinen 2015) and follow-up records from the same or nearby locality are usually separated by decades (Bolotov et al. 2013a).

Finally, this species is largely associated with massifs of undisturbed habitats such as virgin taiga forests and alpine meadows; it is a large, colourful, and popular moth, a 'tiger' among invertebrates. Hence, we recommend considering *A. menetriesii* as a perspective umbrella, indicator, and flagship species for conservation programs, concerning primeval Eurasian taiga forests in both plain and mountain areas.

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Supplementary material 1

Dataset S1

Authors: Ivan N. Bolotov, Mikhail Y. Gofarov, Evgeny S. Koshkin, Vyacheslav V. Gorbach, Yury I. Bakhaev, Oleg E. Berlov, Sergey Y. Gordeev, Tatyana V. Gordeeva, Yulia S. Kolosova, Alexander V. Kondakov, Alexey V. Korshunov, Grigory S. Potapov, Sergey Y. Sinev, Spiridon S. Sleptsov, Vitaly M. Spitsyn, Evgeny G. Strelnikov, Andrey V. Timchenko, Risto Haverinen, Marko Tähtinen, Hannu Saarenmaa

Data type: xlsx.

Explanatory note: Climate variables for collecting localities and regions of *Arctia menetriesii* from 1901 to 2020.

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Link: https://doi.org/10.3897/nl.48.129152.suppl1

Supplementary material 2

Dataset S2

Authors: Ivan N. Bolotov, Mikhail Y. Gofarov, Evgeny S. Koshkin, Vyacheslav V. Gorbach, Yury I. Bakhaev, Oleg E. Berlov, Sergey Y. Gordeev, Tatyana V. Gordeeva, Yulia S. Kolosova, Alexander V. Kondakov, Alexey V. Korshunov, Grigory S. Potapov, Sergey Y. Sinev, Spiridon S. Sleptsov, Vitaly M. Spitsyn, Evgeny G. Strelnikov, Andrey V. Timchenko, Risto Haverinen, Marko Tähtinen, Hannu Saarenmaa

Data type: xlsx.

Explanatory note: Cross-correlation between the time series of *Arctia menetriesii* annual captures and climatic variables (N/A – not applicable).

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Link: https://doi.org/10.3897/nl.48.129152.suppl2

Supplementary material 3

Dataset S3

Authors: Ivan N. Bolotov, Mikhail Y. Gofarov, Evgeny S. Koshkin, Vyacheslav V. Gorbach, Yury I. Bakhaev, Oleg E. Berlov, Sergey Y. Gordeev, Tatyana V. Gordeeva, Yulia S. Kolosova, Alexander V. Kondakov, Alexey V. Korshunov, Grigory S. Potapov, Sergey Y. Sinev, Spiridon S. Sleptsov, Vitaly M. Spitsyn, Evgeny G. Strelnikov, Andrey V. Timchenko, Risto Haverinen, Marko Tähtinen, Hannu Saarenmaa

Data type: xlsx.

Explanatory note: Autocorrelation in the time series of *Arctia menetriesii* annual captures.

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Link: https://doi.org/10.3897/nl.48.129152.suppl3

Supplementary material 4

Dataset S4

Authors: Ivan N. Bolotov, Mikhail Y. Gofarov, Evgeny S. Koshkin, Vyacheslav V. Gorbach, Yury I. Bakhaev, Oleg E. Berlov, Sergey Y. Gordeev, Tatyana V. Gordeeva, Yulia S. Kolosova, Alexander V. Kondakov, Alexey V. Korshunov, Grigory S. Potapov, Sergey Y. Sinev, Spiridon S. Sleptsov, Vitaly M. Spitsyn, Evgeny G. Strelnikov, Andrey V. Timchenko, Risto Haverinen, Marko Tähtinen, Hannu Saarenmaa

Data type: xlsx.

Explanatory note: Host plant preferences of *Arctia menetriesii*.

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Link: https://doi.org/10.3897/nl.48.129152.suppl4

Supplementary material 5

Dataset S5

Authors: Ivan N. Bolotov, Mikhail Y. Gofarov, Evgeny S. Koshkin, Vyacheslav V. Gorbach, Yury I. Bakhaev, Oleg E. Berlov, Sergey Y. Gordeev, Tatyana V. Gordeeva, Yulia S. Kolosova, Alexander V. Kondakov, Alexey V. Korshunov, Grigory S. Potapov, Sergey Y. Sinev, Spiridon S. Sleptsov, Vitaly M. Spitsyn, Evgeny G. Strelnikov, Andrey V. Timchenko, Risto Haverinen, Marko Tähtinen, Hannu Saarenmaa

Data type: xlsx.

Explanatory note: Survival table of *Arctia menetriesii* breeding experiment based on the female AM-066 from the Russian Far East (E.S. Koshkin).

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Link: https://doi.org/10.3897/nl.48.129152.suppl5

Supplementary material 6

Dataset S6

Authors: Ivan N. Bolotov, Mikhail Y. Gofarov, Evgeny S. Koshkin, Vyacheslav V. Gorbach, Yury I. Bakhaev, Oleg E. Berlov, Sergey Y. Gordeev, Tatyana V. Gordeeva, Yulia S. Kolosova, Alexander V. Kondakov, Alexey V. Korshunov, Grigory S. Potapov, Sergey Y. Sinev, Spiridon S. Sleptsov, Vitaly M. Spitsyn, Evgeny G. Strelnikov, Andrey V. Timchenko, Risto Haverinen, Marko Tähtinen, Hannu Saarenmaa

Data type: xlsx.

Explanatory note: Survival table of *Arctia menetriesii* breeding experiments based on the females AM-002 from Finland (H. Krogerus) and AM-037 from Siberia (O.V. Korsun & N.O. Korsun and H. Saarenmaa et al.).

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Link: https://doi.org/10.3897/nl.48.129152.suppl6

Supplementary material 7

Supplementary figures, tables, and note

Authors: Ivan N. Bolotov, Mikhail Y. Gofarov, Evgeny S. Koshkin, Vyacheslav V. Gorbach, Yury I. Bakhaev, Oleg E. Berlov, Sergey Y. Gordeev, Tatyana V. Gordeeva, Yulia S. Kolosova, Alexander V. Kondakov, Alexey V. Korshunov, Grigory S. Potapov, Sergey Y. Sinev, Spiridon S. Sleptsov, Vitaly M. Spitsyn, Evgeny G. Strelnikov, Andrey V. Timchenko, Risto Haverinen, Marko Tähtinen, Hannu Saarenmaa

Data type: pdf.

Explanatory note: **figure S1.** Frequency histograms of *Arctia menetriesii* annual captures by region (1901–2020). **figure S2.** Frequency distribution of bootstrapped Spearman's correlation coefficients of *Arctia menetriesii* population dynamics (B = 1000 replications): (a) Europe vs Siberia (not significant); (b) Europe vs Far East (not significant); (c) Siberia vs Far East (Spearman's $\rho = 0.205$, $N = 121$, $p = 0.024$). **figure S3.** Habitat breadth of Arctia menetriesii categorized by data on the presence of waterbody in a collecting locality. The scales represent the number of collected specimens. **table S1.** Brief summary of four breeding experiments on *Arctia menetriesii*. **table S2.** Confusion matrix of linear discriminant analysis of *Arctia menetriesii* localities by possible odd- and every-year appearance of imago based on monthly mean climate characteristics. Numbers of incorrectly assigned sites are bold. **table S3.** Confusion matrix of linear discriminant analysis of *Arctia menetriesii* localities by region based on monthly mean climate characteristics. **table S4.** List of potential factors and causes that may contribute to the 'extreme rarity' of *Arctia menetriesii*. **note S1.** Additional observations from M. Tähtinen et al.'s breeding experiment of 2018–2019 in Finland.

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Link: https://doi.org/10.3897/nl.48.129152.suppl7